Opinion

The “non-native” enigma

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Abstract: Non-native species have been introduced to ecosystems throughout the world, and in some instances, have degraded the invaded system. Consequently, the distinction between native and non-native species has become an integral component of conservation planning. Recently however, the conservation value of the distinction has been questioned. We examine how the native versus non-native dichotomy is intrinsically ambiguous, which therefore limits the conservation utility of the designation in and of itself. A large degree of uncertainty exists as to whether many species are or are not native. Measures outside the non-native dichotomy (e.g., impacts, evolutionary ecology, paleontology) could better inform conservation efforts, because species' ranges are part of dynamic processes. We recommend that the field of conservation should avoid arbitrary points in history as benchmarks and incorporate findings from multiple disciplines to better manage resources.

Key words: alien, cryptogenic, invasive, native, non-native

Non-native species have been implicated in the destruction of natural ecosystems and extinctions of native species (Dowding and Murphy 2001, Wiles et al. 2003, Simberloff 2011). As such, the dichotomy between native and non-native species has become a critical component of conservation planning that affects many governmental regulatory and funding frameworks available for conservation or species suppression. Nevertheless, the validity of the dichotomy has been called into question as many non-native species do not cause ecological harm, and in some cases provide ecological benefits (Carroll 2011, Davis et al. 2011, Schlaepfer et al. 2011). Moreover, eradication of non-native species is not feasible in many instances, given current technology and economics, and even when possible could have unintended consequences (Norton 2009).

Less explored in the literature is the extent to which species are non-native. In many instances, the non-native dichotomy is clear: zebra mussels (*Dreissena polymorpha*) were introduced to North America from Europe in 1986 (Roberts 1990); house sparrows (*Passer domesticus*) were introduced to North America from England in the mid-19th century (Barrows 1889); and raccoons (*Procyon lotor*) were introduced to Japan from North America during the 20th century (Ikeda et al. 2004). In other cases, however, the recent occurrence of a species in an area may represent a natural or anthropogenically facilitated range expansion, which may in itself be an expansion into previously occupied space. Moreover, geographic ranges are the result of processes that change through time as ecological conditions affect selection. Hence, conservation conducted within the paradigm of static species distributions is problematic. Although many examples exist, 2 species particularly elucidate the potential pitfalls of a nativeness dichotomy and the enigmatic nature of species distributions.

Coyotes (*Canis latrans*) occur throughout most of North America but have generally been represented as non-native in eastern and northern North America, where the recent

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range expansion has been well documented and influenced by multiple factors (Hill et al. 1987, Thurber and Peterson 1991). Although historical records suggest that coyotes are a modern addition to eastern North America, the fossil record indicates that prehistorically, coyotes existed intermittently there (Berta 2001, Nowak 2002), but only when other canids (*C. armbrusteri* and *C. dirus*) were relatively large (Nowak 2002). Canids' evolutionary progression in the New World was predominantly toward increasing body size (Nowak 2002), typically accompanied by specialization of diet (Raia et al. 2012) to hypercarnivory (Finarelli 2007), which leads to a high risk of extinction (Van Valkenburgh et al. 2004). Hence, evolutionary trajectories of other canids likely influenced the intermittent prehistoric occupation of the coyote in eastern North America. Moreover, competitive exclusion plays a role in shaping species distributions (Waters 2011), and although the taxonomic status of red wolves (*Canis rufus*) is of debate, the genetic lineage is proximate to the coyote (vonHoldt et al. 2011). Consequently, extirpation of the red wolf likely contributed to the coyote's recent range expansion into regions intermittently occupied prehistorically. Multiple canid species, including the coyote, clearly existed prehistorically in eastern North America, and complex ecological relationships appear to have influenced current and past distributions.

Other species may have recently colonized space and been mislabeled. The yellow-eyed penguin (*Megadyptes antipodes*) was until recently thought to be a threatened native species and the focus of extensive conservation efforts (Worthy 1997, Moore 2001, Boessenkool et al. 2009). Recent research, however, has demonstrated that the yellow-eyed penguin expanded its range to mainland New Zealand in the last few hundred years after a sister species (*M. waitaha*) became extinct (Boessenkool et al. 2009). Many species in prehistoric New Zealand were susceptible to overexploitation and consequently extinction (Duncan and Blackburn 2004). Remains of *M. waitaha* were found in archaeological context, and extinction was presumably aided by anthropogenic factors (Jones et al. 2008, Boessenkool et al. 2009), a plight similar to several other extinct fauna of New Zealand, most notably the moa (Aves: Dinornithiformes; Holdaway and Jacomb 2000). The yellow-eyed penguin swiftly colonized the vacant range caused by the extinction of *M. waitaha*, likely because competitive pressure had been alleviated (Boessenkool et al. 2009, Waters 2011). The yellow-eyed penguin would typically be designated as non-native on mainland New Zealand, a label that could degrade conservation efforts despite the fact that the global population of the yellow-eyed penguin is small (Boessenkool et al. 2010). Indeed, the yellow-eyed penguin has remained a priority species for conservation efforts (Boessenkool et al. 2010), and replacement of extinct taxa with extant analogs has been proposed for conservation of several ecosystems (e.g., Seddon and Soorae 1999, Parker et al. 2010).

The coyote and yellow-eyed penguin exemplify the difficulty of distinguishing whether some species are native, non-native, or somewhere between. Moreover, some species that are clearly non-native have neutral or positive effects on ecosystems (Carroll 2011, Davis et al. 2011, Schlaepfer et al. 2011), whereas native species can have negative effects on ecosystems (Valéry et al. 2009, Carey et al. 2012). Consequently, we question whether the non-native dichotomy in itself has decisive utility in guiding management actions for species conservation, particularly because the dichotomy informs substantial conservation efforts to kill non-native species worldwide (e.g., Wallach et al. 2015). The use of species distributions at arbitrary points in history as benchmarks for conservation is problematic because it excludes vast amounts of information. Species ranges are dynamic through time and are part of complex ecological processes. Consequently, conservation paradigms should operate within the framework of these dynamic systems to the largest extent possible.

Human activity has affected all systems regardless of whether non-native species exist, and accordingly, mere changes in the ranges of species are inadequate indicators that harm is occurring. Moreover, past distributions of many species are relatively unknown, which obscures designation of species within the native–non-native dichotomy (Carlton 1996). Prehistoric human movements throughout continents and the association of several species with humans further obscure past distributions, particularly since domestication occurred tens of thousands of years ago (e.g., Thalmann et al. 2013). Hence, it is probable in numerous instances that species owe their status as "native" to human activities prior to recorded history or biological censuses (e.g., Haemig 1978, 1979; Ricklefs and Bermingham 2008; Avery et al. 2013).

The ecological context of a species distribution is likely obscured when viewed from the context of any one particular discipline. Consequently, findings from multiple disciplines (e.g., evolutionary ecology, paleontology, invasion biology, conservation genetics) should be consulted to better inform conservation efforts. Ecological impacts could be used as tipping points to guide conservation rather than nativeness (Davis et al. 2011), although explicit definitions of impacts are needed (Jeschke et al. 2014). Evolutionary ecology, paleobiology, and community ecology should be considered when species are affecting new or seemingly new environments. In some instances, eradication of non-natives is unfavorable or not feasible due to finite resources and technology (e.g., Norton 2009). Furthermore, ecological mechanisms could enable coexistence of new species assemblages (e.g., apex predators; Wallach et al. 2015).

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Literature cited

Avery, J. D., D. M. Fonseca, P. Campagne, and J. L. Lockwood. 2013. Cryptic introductions and the interpretation of island biodiversity. Molecular Ecology 22:2313–2324.

Barrows, W. B. 1889. The English sparrow (*Passer domesticus*) in North America, especially in its relations to agriculture. United States Department of Agriculture, Division of Economic Ornithology and Mammalogy. Bulletin 1.

Berta, A. 2001. Mammalia 3: Carnivorans. Pages 188–225 *in* R. C. Hulbert, Jr., editor. The fossil vertebrates of Florida. University Press of Florida, Gainesville, Florida, USA.

Boessenkool, S., J. J. Austin, T. H. Worthy, P. Scofield, A. Cooper, P. J. Seddon, and J. M. Water. 2009. Relict or colonizer? Extinction and range expansion of penguins in southern New Zealand. Proceedings of the Royal Society B: Biological Sciences 276:815–821.

Boessenkool, S., B. Star, P. J. Seddon, and J. M. Waters. 2010. Temporal genetic samples indicate small effective population size of the endangered yellow-eyed penguin. Conservation Genetics 11**:**539–546.

Carey, M. P., B. L. Sanderson, K. A. Barnas, and J. D. Olden. 2012. Native invaders — challenges for science, management, policy, and society. Frontiers in Ecology and the Environment 10:373–381.

Carlton, J. T. 1996. Biological invasions and cryptogenic species. Ecology 77:1653–1655.

Carroll, S. P. 2011. Conciliation biology: the eco-evolutionary management of permanently invaded biotic systems. Evolutionary Applications 4:184–199.

Davis, M. A., M. K. Chew, R. J. Hobbs, A. E. Lugo, J. J. Ewel, G. J. Vermeij, J. H. Brown, M. L. Rosenzweig, M. R. Gardener, S. P. Carroll, K. Thompson, S. T. A. Pickett, J. C. Stromberg, P. D. Tredici, K. N. Suding, J. G. Ehrenfeld, J. P. Grime, J. Mascaro, and J. C. Briggs. 2011. Don't judge species on their origins. Nature 474:153–154.

Dowding, J. E., and E. C. Murphy. 2001. The impact of predation by introduced mammals on endemic shorebirds in New Zealand: a conservation perspective. Biological Conservation 99:47–64.

Duncan, R. P., and T. M. Blackburn. 2004. Extinction and endemism in the New Zealand avifauna. Global Ecology and Biogeography 13:509–517.

Finarelli, J. A. 2007. Mechanisms behind active trends in body size evolution of the Canidae (Carnivora: Mammalia). American Naturalist 170:876–885.

Haemig, P. D. 1978. Aztec Emperor Auitzotl and the great-tailed grackle. Biotropica 10:11–17.

Haemig, P. D. 1979. Secret of the painted jay. Biotropica 11:81–87.

Hill, E. P., P. W. Sumner, and J. B. Wooding. 1987. Human influences on range expansion of coyotes in the Southeast. Wildlife Society Bulletin 15:521–524.

Holdaway, R. N., and C. Jacomb. 2000. Rapid extinction of the moas (Aves: Dinornithiformes): model, test, and implications. Science

287:2250–2254.

Ikeda, T., M. Asano, Y. Matoba, and G. Abe. 2004. Present status of invasive alien raccoon and its impact in Japan. Global Environmental Research 8:125–131.

Jeschke, J. M., S. Bacher, T. M. Blackburn, J. T. A. Dick, F. Essl, T. Evans, M. Gaertner, P. E. Hulme, I. Kühn, A. Mrugała, J. Pergl, P. Pyšek, W. Rabitsch, A. Ricciardi, D. M. Richardson, A. Sendek, M. Vilá, M. Winter, and S. Kumschick. 2014. Defining the impact of non-native species. Conservation Biology 28:1188–1194.

Jones, T. L., J. F. Porcasi, J. M. Erlandson, H. Dallas, T. A. Wake, and R. Schwaderer. 2008. The protracted Holocene extinction of California's flightless sea duck (*Chendytes lawi*) and its implications for the Pleistocene overkill hypothesis. Proceedings of the National Academy of Sciences 105:4105–4108.

Moore, P. J. 2001. Historical records of yellow-eyed penguin (*Megadyptes antipodes*) in southern New Zealand. Notornis 48:145–156.

Norton, D. A. 2009. Species invasions and the limits to restoration: learning from the New Zealand experience. Science 325:569–570.

Nowak, R. M. 2002. The original status of wolves in eastern North America. Southeastern Naturalist 1:95–130.

Parker, K. A., M. Seabrook-Davison, and J. G. Ewen. 2010. Opportunities for non-native ecological replacements in ecosystem restoration. Restoration Ecology 18:269–273.

Raia, P., F. Carotenuto, F. Passaro, D. Fulgione, and M. Fortelius. 2012. Ecological specialization in fossil mammals explains Cope's rule. American Naturalist 179:328–337.

Ricklefs, R. E., and E. Bermingham. 2008. Likely human introduction of the red-legged thrush (*Turdus plumbeus*) to Dominica, West Indies. Auk 125:299–303.

Roberts, L. 1990. Zebra mussel invasion threatens U.S. waters. Science 249:1370–1372.

Schlaepfer, M. A., D. F. Sax, and J. D. Olden. 2011. The potential conservation value of non-native species. Conservation Biology 25:428–437.

Seddon P. J., and P. S. Soorae. 1999. Guidelines for subspecific substitutions in wildlife restoration projects. Conservation Biology 13:177–184.

Simberloff, D. 2011. How common are invasion-induced ecosystem impacts? Biological Invasions 13:1255–1268.

Thalmann, O., B. Shapiro, P. Cui, V. J. Schuenemann, S. K. Sawyer, D. L. Greenfield, M. B. Germonpré, M. V. Sablin, F. López-Giráldez, X. Domingo-Roura, H. Napierala, H. P. Uerpmann, D. M. Loponte, A. A. Acosta, L. Giemsch, R. W. Schmitz, B. Worthington, J. E. Buikstra, A. Druzhkova, A. S. Graphodatsky, N. D. Ovodov, N. Wahlberg, A. H. Freedman, R. M. Schweizer, K. P. Koepfli, J. A. Leonard, M. Meyer, J. Krause, S. Pääbo, R. E. Green, and R. K. Wayne. 2013. Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. Science 342:871–874.

Thurber, J. M., and R. O. Peterson. 1991. Changes in body size associated with range expansion in the coyote (*Canis latrans*). Journal of Mammalogy 72:750–755.

Valéry, L., F. Hervé, J. C. Lefeuvre, and D. Simberloff. 2009. Invasive species can also be native. Trends in Ecology and Evolution 24:585.

Van Valkenburgh, B., X. Wang, and J. Damuth. 2004. Cope's rule, hypercarnivory, and extinction in North American canids. Science 306:101–104.

vonHoldt, B. M., J. P. Pollinger, D. A. Earl, J. C. Knowles, A. R. Boyko, H. Parker, E. Geffen, M. Pilot, W. Jedrzejewski, B. Jedrzejewska, V. Sidorovich, C. Greco, E. Randi, M. Musiani, R. Kays, C. D. Bustamante, E. A. Ostrander, J. Novembre, and R. K. Wayne. 2011. A genome-wide perspective on the evolutionary history of enigmatic wolf-like canids. Genome Research 21:1294–1305.

Wallach, A. D., W. J. Ripple, and S. P. Carroll. 2015. Novel trophic cascades: apex predators enable coexistence. Trends Ecology and Evolution 30:146–153.

Waters, J. M. 2011. Competitive exclusion: phylogeography's "elephant in the room"? Molecular Ecology 20:4388–4394.

Wiles, G. J., J. Bart, R. E. Beck, Jr., and C. F. Aguon. 2003. Impacts of the brown tree snake: patterns of decline and species persistence in Guam's avifauna. Conservation Biology 17:1350–1360.

Worthy, T. H. 1997. The identification of fossil *Eudyptes* and *Megadyptes* bones at Marfells Beach, Marlborough, South Island. New Zealand Natural Sciences 23:71–85.

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